The baculum

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What is a baculum? The baculum (*os penis*) is a bone found within the penis of certain mammals, including many primates, rodents, bats, carnivores, and some insectivores. It is an isolated bone, derived from connective tissue and located at the distal end of the penis, above the urethra. Lower mineral density and reduced stiffness of the baculum compared to skeletal bones may help reduce the risk of fracture under strain during copulation, although breakage can sometimes occur.

You mentioned primates, do we humans have such a bone? No, human males don't have a baculum! This is surprising because all other apes and Old World monkeys have one, despite a trend towards reduced size of the baculum among the great apes. As fossil primate bacula are extremely rare, it is unknown when the baculum was lost within the hominid lineage. And despite some speculation relating to upright posture and changing mating strategies, why human males lack a baculum remains enigmatic.

What does it look like? A particularly striking characteristic of the baculum is its extreme anatomical diversity. Bacula of different species come in a multitude of forms, with variation in their length, thickness, curvature and complexity of shape (Figure 1). The baculum can also be small or large relative to body size, reaching more than 60 cm in the walrus, *Odobenus rosmarus*. More complex forms may feature bizarre looking teeth or digit-like projections, including components that protrude from the *glans penis* in certain rodents. Such diversity of form makes the baculum a particularly useful feature for species identification and taxonomy.

What is it for? Although the baculum was first identified in the seventeenth century, its exact functional significance is still unclear. Multiple functions seem plausible: for example, a baculum may provide mechanical support for the penis, assist in overcoming vaginal resistance or protect the urethra from compression during copulation. Consistent with a role in mechanical support, certain primates and carnivore species that have prolonged copulation also have a longer baculum. A role in female stimulation also seems likely, particularly in species where copulation is prolonged with multiple intromissions, thrusting or multiple ejaculations. Copulatory stimulation can have important consequences for reproduction as it may facilitate sperm transport and affect female sexual receptivity, as well as stimulate ovulation or initiate pregnancy. The baculum may help stimulate such responses, either directly (where it extrudes from the tip of the glans penis) or indirectly (via mechanical support or influence on penile morphology). Interestingly, complementary female structures have been discovered in ground squirrels (*Spermophilus* spp.), where the protruding teeth of the baculum apparently interdigitate with folds in the vagina during copulation.

Why are bacula so diverse? The baculum has long been a bone of contention, not least because such diversity of form has proved difficult to explain. One now largely discounted hypothesis was that the diversity of bacula is a non-adaptive by-product of selection on other traits. Nowadays it is believed that the baculum and penis are subject to direct selection as a result of their role in copulation.

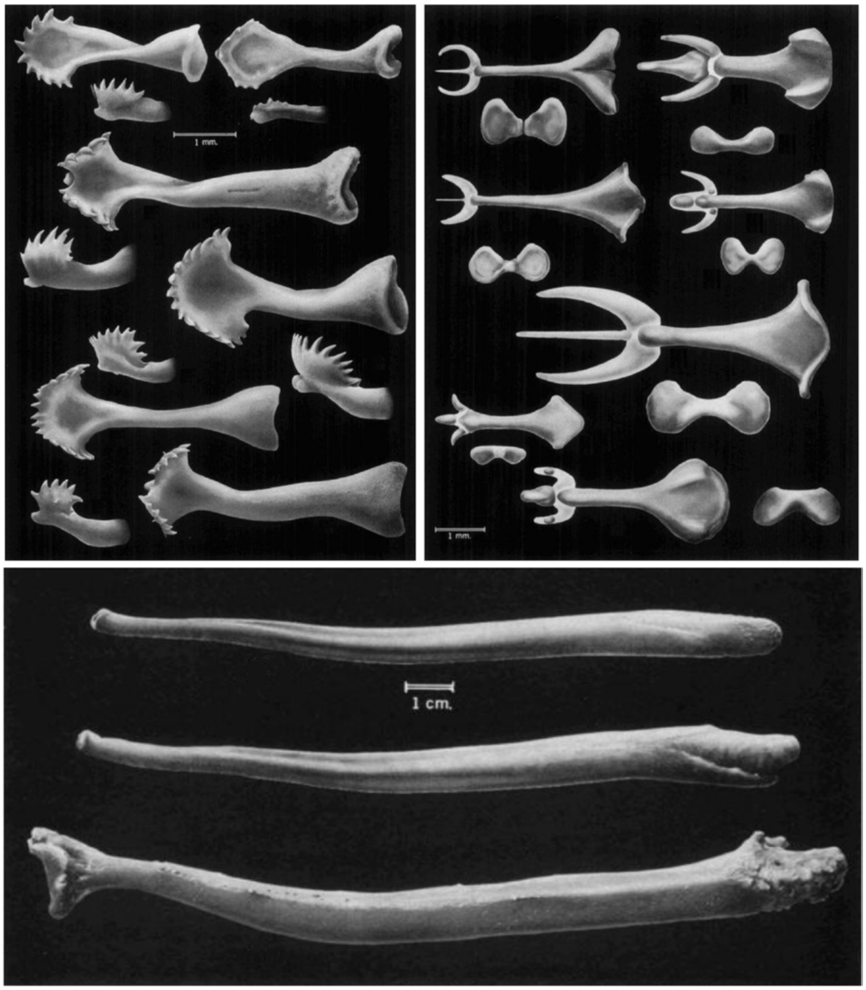

Figure 1. Diversity of bacula.
Examples of bacula of North American mammals. Top left: bacula of ground squirrels (*Spermophilus* sp.) with spoon-shaped distal ends and tooth-like projections. Top right: trident shaped bacula of rice rats (*Oryzomys* sp.) and voles (*Microtus* sp.); illustrations demonstrate complexity of bacula shape from different perspectives. Bottom: relatively simple bacula of some large carnivores (two bear species (*Ursus*) illustrated above a sea lion (*Zalophus*)). Illustrated by William L. Brudon, reproduced with permission from Burt (1960).

Historically, much interest focused on the potential role of mammalian genitalia in promoting reproductive isolation of species. The 'lock and key hypothesis', for instance, proposed that genitalia are radically different between species in order to prevent interspecific mating and hybridization. A variant of this hypothesis is that bacula of different shapes elicit different responses from females during copulation, and that only species-specific stimulation will lead to successful reproduction.

How did the diverse bacula evolve then? Most recent attention has focused on the idea that rapid and divergent evolution of male genital morphology, including the baculum, is driven by sexual selection. This applies particularly to species where females mate with multiple males, as is very common among mammals. There are ways in which the baculum could influence sexual selection: for example, females might bias fertilisation in favour of males whose baculum (and penis) stimulates them most during copulation, a process known as 'cryptic female choice'. Also, females may reliably assess male size or quality based on the baculum. Being able to assess male quality during copulation could be of particular benefit when opportunities for quality assessments before mating are limited, such as when copulation takes place underwater or underground. Baculum evolution could also be influenced by sperm competition. For example, the baculum might help deliver sperm optimally or displace the ejaculates of rival males. By supporting prolonged intromission after ejaculation, a baculum might also help males to reduce the risk that females will mate again with others.

Is there evidence for these ideas? There are some indications. For instance, if a larger baculum is advantageous in sperm competition, baculum size should be greater among species with more intense sperm competition. The correlation varies between groups, as might be expected if the baculum functions differently across taxa: more intense competition appears to favour a longer baculum among rodents and carnivores, but not among bats and primates. Also, sexually selected traits may show high phenotypic variance relative to non-sexual traits and scale positively in relation to body size. Indeed, in the muskrat (*Ondatra zibethicus*) large males have relatively larger bacula than small males and baculum traits (especially width) are particularly variable between males. However, high levels of variation and positive allometry are not necessarily a consequence of sexual selection. Baculum morphology has also been linked to male social status in the bank vole (*Myodes glareolus*). Dominant males have wider bacula than subordinates relative to their body size, which might at least partly explain the superior success of dominant males in sperm competition.

Do females have something similar to the baculum? Females do indeed have a homologous bone, the baubellum or *os clitoridis*, which is present in the clitoris of most if not all species with a baculum. It is usually a small bone with the appearance of an underdeveloped baculum, but it can sometimes be relatively large, as in the ring-tailed lemur (*Lemur catta*) where the baubellum is nearly half the length of the baculum. Unfortunately, even less is known about the baubellum than about the baculum...

Where can I find out more?

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Primer

Behavioral architecture of the cortical sheet

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The effortless ability of vertebrates to explore and exploit their environment is strongly correlated with the evolution of the most anterior part of their nervous system, the forebrain, where data from autonomic (visceral), limbic (emotive), and internal and peripheral sensors of the external world are combined to develop, decide, and deploy advantageous behaviors. The correlation of behavioral performance with forebrain expansion suggests that evolution has discovered the developmental means of building vertebrate brains to produce a scalable, special-purpose architecture for efficiently processing and expressing behavior. In mammals, the exuberant expansion of this forebrain is dominated by the growth of their cortex — the two-dimensional sheet that is the major source of their intelligent behavior, especially for primates.

The complexity of the brain is so overwhelming that at every level investigators have been forced to focus only on particular aspects of its evolution and development, or its structure and function, or the behavior it generates. However, over decades all these individual brushstrokes have accumulated to produce a surprisingly coherent and conceptually simple picture of the interrelationships of evolution, development, and brain organization to produce what we call here, the 'behavioral architecture' of the cortical sheet. In this primer we locate our current state of knowledge in a single conceptual framework that unifies these seemingly disparate fields of investigation. We show that while the relations between different parts of the sheet may be complex, they are not arbitrary, not least because the actual physical organisation of the cortical sheet itself defines a coherent logic by which effective